Metapopulation structure and dynamics of an endangered butterfly

Margaret S. Guiney[a,*], David A. Andow[b], Timothy T. Wilder[c]

[a]*Department of Conservation Biology, 200 Hodson Hall, University of Minnesota, St. Paul, MN 55108, USA*
[b]*Department of Entomology, 219 Hodson Hall, University of Minnesota, St. Paul, MN 55108, USA*
[c]*Ft. McCoy, United States Army Base, 110 E. Headquarters Road, Ft. McCoy, WI 54656, USA*

Abstract

Recovery plans for endangered invertebrates will improve with a better understanding of population dynamics and structure. Some spatially distributed structures beyond the classic metapopulation, including highly integrated patchy populations and core-satellite, maybe better suited for the recovery of endangered populations. In this study we examined the population dynamics of the Karner blue butterfly, *Lycaeides melissa samuelis* (Nabokov) [Lepidoptera: Lycaenidae], which is federally endangered in the USA, at eleven sites at Fort McCoy, Wisconsin. Adult *L. m. samuelis* butterflies were surveyed approximately weekly at each site using a straight line transect method. We used autocorrelation and partial autocorrelation function to look for patterns in the population dynamic, and tested for density-dependent growth and weather factors as potential explanatory factors of the yearly variation. We found non-declining or stable Karner blue populations at all eleven sites at Fort McCoy, a long-term trend and an alternating generational cycle. The trend occurred at seven of the eleven sites and was synchronous, suggesting that Karner blue butterflies were not functioning as a classic metapopulation and maybe functioning as a patchy metapopulation. We also found density-dependent growth and a positive relationship between early summer precipitation and population growth from the spring to summer generation. We suggest that aiming to recover patchy metapopulations will reduce monitoring costs, simplify reserve design, and create more robust populations, which are more likely to persist into the future.

Zusammenfassung

Regenerationsprogramme für gefährdete Wirbellose werden sich durch ein tieferes Verständnis der Populationsdynamik und struktur verbessern. Einige räumlich verteilte Strukturen jenseits der klassischen Metapopulation, darunter hoch-integrierte fleckenhafte Populationen und Kern-Satellit-Konzepte, könnten besser für die Wiederherstellung von gefährdeten Populationen geeignet sein.

Wir untersuchten die Populationsdynamik des Karner-Bläulings, *Lycaeides melissa samuelis* (Nabokov) [Lepidoptera: Lycaenidae], der in den USA bundesweit gefährdet ist, auf elf Arealen von Fort McCoy, Wisconsin. Die adulten *L. m. samuelis* wurden ungefähr wöchentlich auf jedem Areal mit der Transektlinien-Methode untersucht. Wir setzten Autokorrelation und partielle Autokorrelation ein, um nach Mustern in der Populationsdynamik zu suchen, und testeten dichteabhängiges Wachstum und Witterungsfaktoren als potentielle erklärende Steuergrößen für die jährliche Variation.

Wir fanden nicht-abnehmende bzw. stabile Populationen des Karner-Bläulings auf allen elf Arealen auf Fort McCoy, einen langfristigen Trend und alternierende Generationszyklen. Der Trend zeigte sich auf sieben der elf Areale und war synchron, was nahelegt, dass die Karner-Bläulinge nicht als klassische Metapopulation funktionieren, und dass sie als fleckenhafte

*Corresponding author. Tel.: +1 612 721 5373; fax: +1 612 625 5299.
E-mail address: sava0080@umn.edu (M.S. Guiney).

Report Documentation Page		*Form Approved* *OMB No. 0704-0188*

Public reporting burden for the collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington VA 22202-4302. Respondents should be aware that notwithstanding any other provision of law, no person shall be subject to a penalty for failing to comply with a collection of information if it does not display a currently valid OMB control number.

1. REPORT DATE **05 SEP 2009**	2. REPORT TYPE	3. DATES COVERED **00-00-2009 to 00-00-2009**
4. TITLE AND SUBTITLE **Metapopulation structure and dynamics of an endangered butterfly**		5a. CONTRACT NUMBER
		5b. GRANT NUMBER
		5c. PROGRAM ELEMENT NUMBER
6. AUTHOR(S)		5d. PROJECT NUMBER
		5e. TASK NUMBER
		5f. WORK UNIT NUMBER
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) **Department of Conservation Biology,200 Hodson Hall, University of Minnesota,St. Paul,MN,55108**		8. PERFORMING ORGANIZATION REPORT NUMBER
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)		10. SPONSOR/MONITOR'S ACRONYM(S)
		11. SPONSOR/MONITOR'S REPORT NUMBER(S)

12. DISTRIBUTION/AVAILABILITY STATEMENT
Approved for public release; distribution unlimited

13. SUPPLEMENTARY NOTES

14. ABSTRACT

15. SUBJECT TERMS

16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT	18. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON
a. REPORT **unclassified**	b. ABSTRACT **unclassified**	c. THIS PAGE **unclassified**	**Same as Report (SAR)**	**9**	

Metapopulation funktionieren könnten. Wir fanden außerdem dichteabhängiges Wachstum und einen positiven Zusammenhang zwischen dem Niederschlag im Frühsommer und dem Populationswachstum von der Frühjahrs-zur Sommergeneration.

Wir meinen, dass die Regeneration von fleckenaften Metapopulationen die Monitoring-Kosten senken, das Schutzgebietsdesign vereinfachen und stabilere Populationen hervorbringen wird, die mit nöherer Wahrscheinlichkeit langfristig persistieren können.

Introduction

Metapopulation theory has been remarkably instructive for understanding and managing rare or endangered species including amphibians (Marsh & Trenham 2001), birds (Opdam 1991), fish (Lafferty, Swift, & Ambrose 1999), insects (Hanski, Moilanen, Pakkala, & Kuusaari 1996), mammals (Lawes, Mealin, & Piper 2000), and plants (Husband & Barrett 1996). The classic metapopulation, also known as the Levins metapopulation, is a population structure where individual population sites have asynchronous dynamics and where sites experience relatively high rates of extinction and re-colonization events (Levins 1970). The classic metapopulation theory has been criticized due to its limited practical applicability because few species have this specific population dynamic (Baguette 2004). In response, Hanski (2004) argues that metapopulation theory and models can help researchers understand spatial concepts and identify the key population processes. In this paper we build on this dialog and consider spatially distributed population structures in addition to the classic metapopulation, including highly integrated patchy populations and core-satellite or mainland-island populations (Boorman & Levitt 1973; Hastings & Harrison 1994) for Karner blue butterfly, a USA federally endangered species (U.S. Fish and Wildlife Service 2003).

These other spatially distributed metapopulation structures maybe better suited as recovery goals for some endangered arthropod populations. Persistence of a classic metapopulation requires a delicate balance between the rate of extirpation of local populations and the rate of colonization, which determines the equilibrium prevalence of the population (Hastings & Harrison 1994). In comparison, patchy or core-satellite population structures have increased movement between habitat sites and persistence maybe related to a spatial scale of the population for a patchy metapopulation (Hanski 1991) or the persistence of the core population for a core-satellite metapopulation (Harrison, Murphy, & Ehrlich 1988). Indeed, by focusing on a core population or increasing the spatial scale of the metapopulation, limiting factors can be identified that may help to direct and improve conservation efforts for an imperiled species (Ehrlich, White, Singer, McKechnie, & Gilbert 1975) while reducing monitoring costs, simplifying reserve design, and creating more robust populations.

Karner blue butterfly, *Lycaeides melissa samuelis* (Nabokov) [Lepidoptera: Lycaenidae], is the most widely geographically distributed and locally abundant of all the federally endangered arthropod species in the USA (Andow, Baker, & Lane 1994). Thus, it is possible that this species could be recovered into highly robust populations. In this paper we analyze the population dynamics of *L. m. samuelis* at eleven sites at Fort McCoy, Wisconsin over six years (12 butterfly generations) to evaluate the historical constancy of the population, and by comparing these temporal trajectories, we conclude that these populations are unlikely to be functioning as a classic metapopulation. Moreover, we suggest that recovery of this species should include management to maintain a healthy core population around which additional areas contributing to a larger viable population can be supported.

Materials and methods

Study organism and study area

Karner blue butterfly, *L. m. samuelis*, is a federally endangered butterfly (U.S. Fish and Wildlife Service 2003) inhabiting the disappearing oak savanna and pine barrens ecosystems in North America (Andow et al. 1994). Karner blue butterfly is believed to have thrived historically in a classic metapopulation structure, maintained on a shifting landscape renewed by fire (Givnish, Menges, & Schweitzer 1988; Schweitzer 1994). A case has been made to base recovery of this species near its type locality in east central New York State on this classic metapopulation model, specifying minimum population size, spatial area and fire-based renewal rates (Givnish et al. 1988).

The phenology of *L. m. samuelis* is linked to its exclusive larval food species, the perennial wild lupine (*Lupinus perennis* L.) (Fabaceae). In late April/early May, *L. m. samuelis* eggs hatch into larvae that live on and consume *L. perennis* leaves for approximately three weeks. Larvae, especially older instars, and pupae are tended by ants (Savignano 1994). In late May/early June, the spring flight adults emerge and feed on nectar from numerous flower species (U.S. Fish and Wildlife Service 2003). The females lay eggs individually on *L. perennis* stems and leaves. The mean adult life span has been estimated by mark release recapture data to be four days, but other data indicate that this is an underestimate (Brown & Boyce 1996; U.S. Fish and Wildlife Service 2003; Guiney & Andow 2009). The summer flight adults emerge in late July/early August and females lay eggs on *L. perennis* and

nearby vegetation, and these eggs will overwinter and hatch the following spring (U.S. Fish and Wildlife Service 2003).

The 24,282 ha U.S. Department of Defense Army military training base, Fort McCoy (44°01′N, 90°41′W), is located in southwest Wisconsin, where *L. m. samuelis* populations have been documented on 95% of approximately 15 km^2 of the mapped *L. perennis* (Maxwell 1998). In 1996, eleven *L. m. samuelis* sites at Fort McCoy were chosen for long-term monitoring because they had relatively high adult butterfly densities. Five of these sites are in the north Fort, five are in the south Fort in a large area of fairly contiguous lupine, and one is in the southwest corner of the Fort with no lupine connecting it to the main south Fort area for about 3 km (see Appendix A: Fig. 1). Sites are identified by a letter and a number based on the training areas where they are located.

Lycaeides melissa samuelis surveys

Fort McCoy staff developed their monitoring plan and protocols by following recommendations in the Wisconsin Habitat Conservation Plan (Watermolen et al. 2000). These recommendations were developed from a study specifically focused on determining appropriate sampling intervals and total sampling duration for Karner blue butterflies using straight line transects (Brown & Boyce 1996). Permanent straight line transects were established at each site, and site boundaries were designated by including areas where *L. m. samuelis* had been observed in close proximity to both *L. perennis* and nectar plants. The first straight line transect was located randomly and additional transects were placed 20–40 m apart depending on the site size. Monitoring began in 1996 and occurred approximately once every seven days spanning the flights of the two adult generations each year, except 1996 and 1997, when only the larger summer generation was surveyed. In 1996, only two sites were surveyed but this increased to all eleven sites by 1999. Sampling followed a standard protocol including avoiding inclement weather conditions (Wilder 1999) and about 95% of the survey data were collected by a single person. Site specific management and disturbance histories between 1997 and 2004, and a description and justification of the sampling methods are provided in Appendix A.

Population fluctuations and analysis of dynamics

We used trapezoidal integration to compute the area under the butterfly count versus date curve to summarize the multiple surveys at each site for each generation into a single population density index (Manly 1976). When necessary, we extrapolated the survey data to zero population size at each end of the phenology curve, using a seven day sampling interval. If the first or last observation was very high (>60 butterflies), we extrapolated the zero time to fourteen days. We transformed the population index to natural logarithms to account for exponential population growth. This population density index is not the same as population size. The index is the total number of butterfly-days at a site for a generation and is influenced by immigration and emigration. One possible biological interpretation of the index is the number of eggs laid in the site by adults for the entire generation. If sex ratio and daily per capita fecundity were similar across generations, the index would be proportional to egg abundance oviposited to start the next generation.

We used autocorrelation (ACF) and partial autocorrelation function (PACF) to analyze the population dynamics occurring at each site that are difficult to observe in the original time series (Turchin & Taylor 1992). The ACF shape of an unregulated population is consistent with a random walk, and the autocorrelation values (ACs) will slowly dampen to zero. The ACs of a regulated and stationary population will dampen quickly to zero, while the ACs of a population that is regulated with a long-term trend in the population will dampen slowly. A random walk can be differentiated from a trending population by detrending the data; the detrended ACs will dampen faster than the original ACs for the trending population (Royama 1992).

The PACF graphs remove the correlation that occurs due to the lower order correlations in the ACF. A significant partial autocorrelation (PAC) value occurs when the line is outside the 95% confidence interval (Barlett bands) and reveals the minimum number of independent factors that need to be included in a population model (Turchin & Taylor 1992). The ACFs and PACFs were calculated on the original and detrended data in Excel following methods in Royama (1992).

To assess whether population patterns were affected by site area, we regressed the mean population index on area of each site. Area was estimated by multiplying the total transect length by the distance between transects.

Between-generation population change

We calculated between-generation population change as the difference between the ln transformed population indexes of the sequential flights for each site ($n = 55$ site-year combinations for each generation transition). This value of between-generation population change is equal to the ln of the "net population growth rate per butterfly day". Because the population density index is in units of butterfly-days, a positive net growth rate could result from an increase in the number of butterflies or an increase in the number of days a butterfly remains alive and stays in the sampled habitat. A positive net growth rate could occur when butterfly numbers decreased if the number of days that butterflies survived and stayed in the habitat increased enough. Net growth rate measures changes in the number of butterflies that are observed during an entire flight, including resightings. We calculated the mean ln net population growth rate per butterfly-day for all sites in the same year ($n = 5$ years). We back-transformed

means and confidence intervals to the arithmetic scale, to show the net population growth rate per butterfly-day.

We also used ln net population growth rate to test for density-dependent growth among sites within a generation in a year. To make the population index comparable across sites, we divided the population index by the total transect length at each site, and then ln transformed this population density index. We then regressed the subsequent net population growth rate on this population density index for the spring and summer generations separately. We used a general linear model in SAS to test for density-dependent growth (SAS Institute 1997) with year as a factor, sites as replicates and allowing annual variation in the strength of density dependence.

In addition, we examined several weather variables as potential explanatory factors of the yearly variation of between-generation population change. We utilized weather data from the closest accessible NOAA weather station (43°56′N/90°49′W), 20 km west of the Fort McCoy headquarters (Sparta station, http://www.ncdc.noaa.gov). We used a general linear model in SAS (SAS Institute 1997) to regress ln net population growth rate and weather variables. For the spring-to-summer generation change, we examined the following variables: cumulative rainfall (1 June–31 July), mean air temperature in June, and mean air temperature in July.

For the summer-to-spring (overwinter) generation change we examined precipitation, temperature, and precipitation combined with temperature [precipitation: winter snow (total snowfall 1 November–31 March, number of days with continuous snow cover at 2.54 cm or above), spring cumulative rainfall (15 April–31 May); air temperature: fall heat (number of days when daily maximum air temperature exceeded 29 °C between 1 August and 30 September), winter cold (number of days daily minimum air temperature <-23 °C), spring average (mean temperature 1–31 May); precipitation combined with temperature in the winter (number of days daily minimum temperature <-12 °C regardless of snow cover and number of days daily minimum temperature <-12 °C without at least 2.54 cm of snow cover)]. The winter temperatures, -12 °C and -23 °C, were chosen to test the effect of moderate and extreme cold air temperatures.

Results

Population fluctuations and analysis of dynamics

The original time series data of the population index (Fig. 1: population series, ACF, and PACF) illustrated two patterns: a long-term trend and an alternating generational
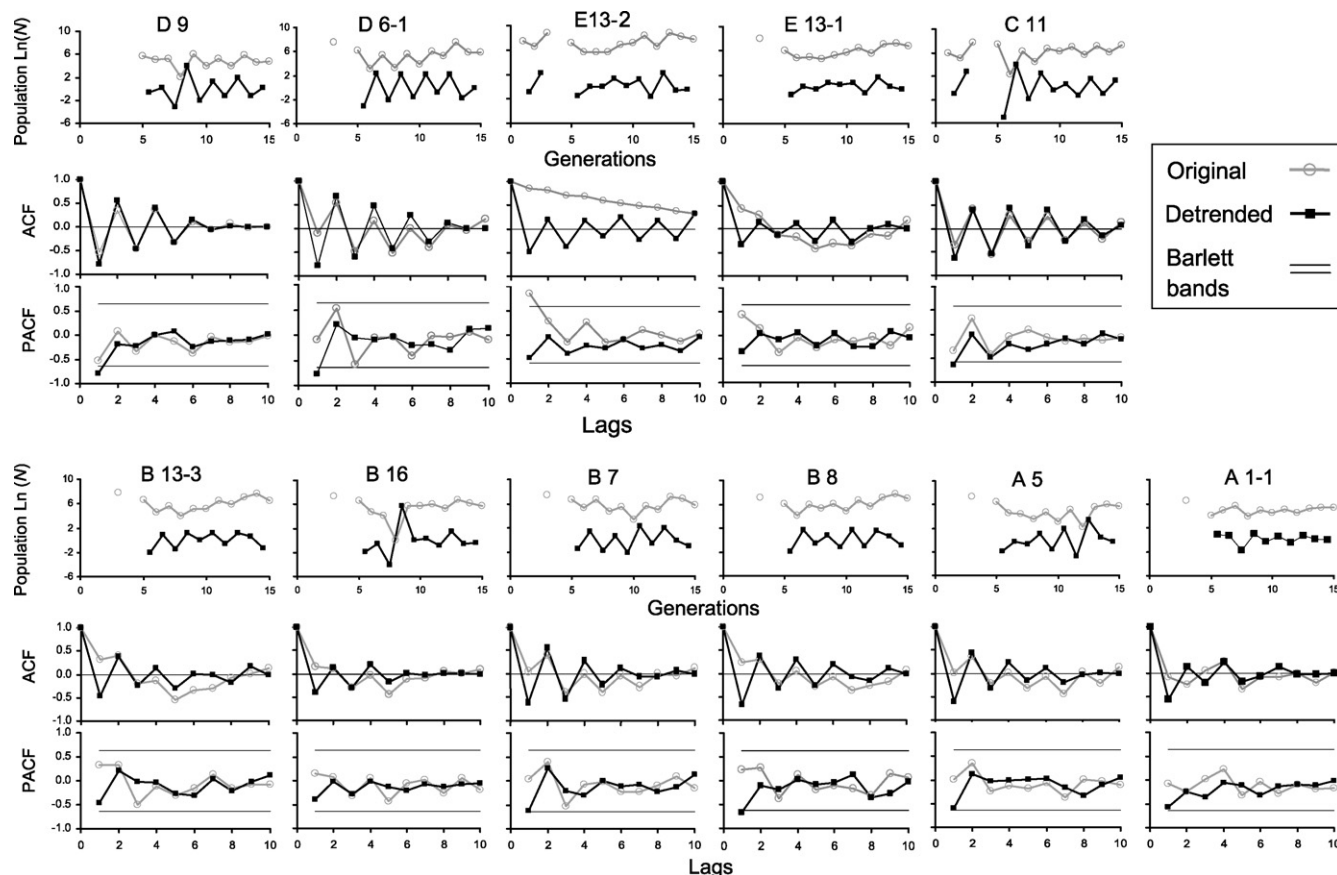

Fig. 1. Population series, autocorrelation functions (ACFs) and partial autocorrelation functions (PACFs) for *Lycaeides melissa samuelis* at 11 sites at Fort McCoy.

cycle. The original time series data in the population series and ACF graphs showed a U-shaped pattern indicating a long-term trend for seven of the eleven sites: A5, B7, B16, B13-3, B8, E13-1, and D6-1 (Fig. 1). For these sites, the ACF generally decreased for generational lags one to five, then increased between lag six through ten. Site E13-1 illustrated this pattern particularly well while other sites, similar to B8, still showed this U-shaped pattern but the curve was not as smooth. Generally the first generation in the population series had the highest population index, and then the index dropped and reached its lowest value in the middle of the times series. This was followed by an increase that reached a higher value near the end of the time series. Because this U-shape was consistently evident at multiple sites, it suggested the presence of a long-term trend with a half period length of approximately five generations. After the data were detrended, the U-shape pattern was eliminated and the detrended ACF graphs oscillated around and damped to zero (Fig. 1).

The remaining four sites did not show a long-term population trend. Although we cannot rule out the possibility that these sites also trended with the others, the long-term population dynamics for three sites (A1-1, C11, and D9) tended to fluctuate around a constant population index. Site E13-2 was somewhat anomalous in that it showed an increasing trend in the population index. Three of these four sites occurred in the northern part of Fort McCoy (see Appendix A: Fig. 1), and one (A1-1) occurred in the extreme southwest corner of the property. Both the southwest corner and the northern sites are at least 3 km from the large group of sites in contiguous lupine area in the south Fort. All of these more isolated sites had detrended ACF graphs that oscillated around and mostly damped to zero.

The alternating generational pattern was most evident in the ACFs. At all eleven sites in the detrended ACF graphs, the generation lag one was a negative correlation, while lag two was positive, and this alternating pattern continued with most odd lags showing a negative correlation while even lags were positive. These observations correspond to the typical pattern of a larger summer adult flight compared to the spring flight. Odd lags, which compared summer-to-spring and spring-to-summer flights, were negatively correlated, and even lags, which compared summer-to-summer and spring-to-spring flights, were positively correlated.

The PACF graphs also illustrate the dramatic difference between the original and the detrended data. At lag one, the original series PACFs showed a mix of positive and negative PACs, while for the detrended data, all the sites illustrated a strong negative PAC value (Fig. 1). Furthermore site E13-2 showed a significant positive PAC at lag one but after detrending this changed to a negative correlation. In addition, within the original data no sites had significant negative PACs, but the detrended data showed four sites (C11, B8, D6-1, and D9) with significant negative PACs at lag one. This means at least one independent factor affected population dynamics of lag one at these sites.

These results indicate that the alternate generational pattern was partially masked in the original population series by the long-term trend. This long-term trend also affected the strength of the ACs and PACs. When the original data were detrended, the alternate generational pattern was more noticeable in both the population series and the ACF and PACF graphs.

We examined site area as a potential explanation for the variation between sites, but we did not find any patterns. We did not find a relationship between site area and the mean population index for each site ($R^2 = 0.0027$, $P > 0.05$). Also the four sites (A1-1, C11, D9, and E13-2) that did not clearly show the long-term population trend were not similar in area or mean population index.

Between-generation population change

To quantify the alternating generational pattern illustrated by the ACFs and PACFs, we estimated the seasonal change from the spring to the summer generation (net population growth rate per butterfly-day) equal to 2.13 with a 95% CI of [0.034, 8.46] (backtransformed). This means that during an average year the butterfly flight doubles from the spring to the summer flight. However, this value is deceiving because there is no average year and the 95% confidence interval spans from zero to an eightfold change. Furthermore, one of the five years, 2003 was outside of the 95% confidence interval.
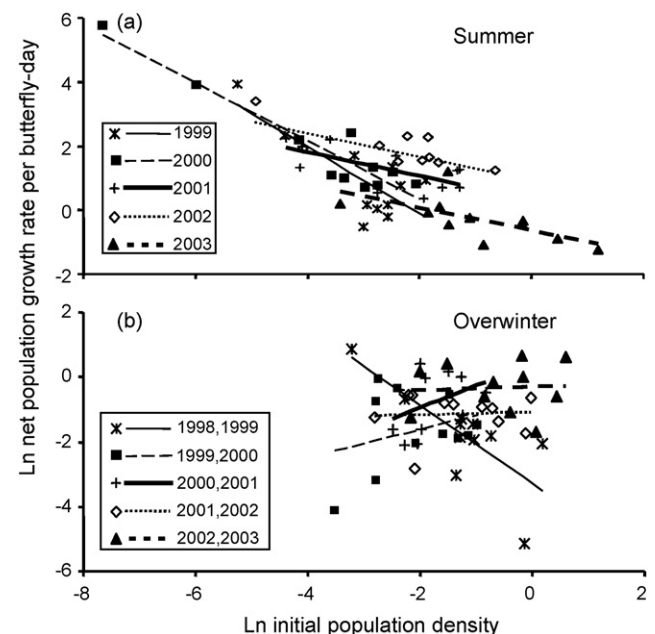

Fig. 2. Regressions by year of generation population change at a site and initial population density index at the site. Both axes are ln transformed. (a) Generational change from spring to summer flight related to spring population density index. (b) Generational change from summer flight to the spring flight of the next year related to summer population density index.

Table 1. Analysis of variance of year and initial population density for each generation change.

Source	d.f.	Type I SS	F	P
Summer				
Year	4	34.96	22.44	**<0.0001**
Density	1	32.19	82.64	**<0.0001**
Density × year	4	7.02	4.50	**0.0038**
Error	45	17.53		

Year	Slope	SE	T	P
1999	−1.04	0.20	−5.16	**<0.0001**
2000	−0.91	0.12	−7.68	**<0.0001**
2001	−0.37	0.16	−2.31	**0.0254**
2002	−0.36	0.17	−2.17	**0.0355**
2003	−0.35	0.16	−2.25	**0.0294**

Source	d.f.	Type I SS	F	P
Overwinter				
Year	4	68.98	19.06	**<0.0001**
Density	1	1.03	1.14	0.2916
Density × year	4	14.35	3.97	**0.0077**
Error	45	40.71		

Year	Slope	SE	T	P
1998–1999	−1.21	0.33	−3.73	**0.0005**
1999–2000	0.44	0.36	1.21	0.2339
2000–2001	0.69	0.57	1.21	0.2329
2001–2002	−0.13	0.33	−0.41	0.6869
2002–2003	0.06	0.32	0.18	0.8602

Bold P values are statistically significant ($P < 0.05$).

Table 2. Regression analysis on weather variables and ln net population growth rate per butterfly-day.

	F	P
Summer weather variables		
Rainfall, ln, 6/1–7/31	19.66	**<0.001**
Air temp., mean, 6/1–6/30	2.21	0.1445
Air temp., mean, 7/1–7/31	0.19	0.6632
Overwinter weather variables		
Snowfall, ln, 9/1–3/31	1.79	0.1864
Days of continuous snow cover, ln, 9/1–3/31	1.35	0.2515
Days min. temp. <−23 °C, ln, 9/1–3/31	0.65	0.4245
Days min. temp. <−12 °C, w/o snow, ln, 9/1–3/31	9.37	**0.0038**
Days min. temp. <−12 °C, ln, 9/1–3/31	8.59	**0.0054**
Days max. temp. >29 °C, ln, 8/1–9/30	2.24	0.1418
Air temp., mean, 5/1–5/31	4.03	0.0509
Rainfall, ln, 4/15–5/31	0.54	0.4651

Bold P values are statistically significant ($P < 0.05$).

Fig. 3. Regressions by sites of generation population change from spring to summer flight on June and July rainfall (cm). Both axes are ln transformed.
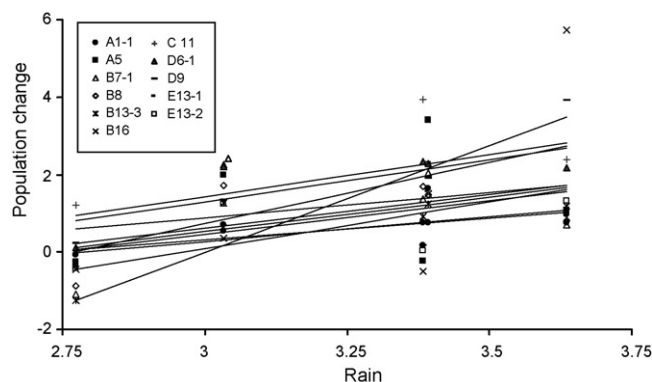
Negative density-dependent population growth was consistently observed during the summer and sporadic during the overwinter period (Table 1 and Fig. 2). For the summer period, we consistently found negative slopes and all slopes were significantly different than zero (Fig. 2A). The slope values varied among years indicating that the strength of density-dependence varied from one year to the next. Density-dependence was stronger in 1999 and 2000, and weaker in 2001, 2002, and 2003. In comparison, for the overwinter period we did not find consistent overall density-dependent growth but did find significant variation among overwinter periods (Fig. 2B). Only one winter, 1998–1999, showed evidence of negative density-dependent growth and all other overwinter periods had no evidence of density-dependent growth.

During the summer period, we found a significant positive relationship between net population growth rate and early summer rainfall (Table 2 and Fig. 3). This relationship indicated that as the amount of precipitation increased, the net population growth rate from spring to summer also increased. During the overwinter generation, we found a surprising significant positive relationship between net population growth rate and the number of days with cold temperatures (<−12 °C

and <−12 °C without snow cover). These results imply that increased exposure to cold temperatures may increase egg survival. This relationship was strongly influenced by an unusual year with a high number of cold days and a positive net population growth rate. Therefore this result maybe spurious and unlikely to predict future relationships. This result was inconsistent with the other regression results using cold and snow data, which showed no relationship (Table 2).

Discussion

Spatial population structure

Hastings and Harrison (1994) suggested that spatially distributed populations can exist in several configurations,

including a classic metapopulation structure (Levins 1970) or a core-satellite structure (Boorman & Levitt 1973). In addition, if dispersal among patches and population persistence on patches is high, a spatially distributed population can also exist as a patchy population. Prior to considering management options, a critical step is to empirically determine the spatial population structure of an endangered species.

Our analysis suggests that the endangered Karner blue butterfly functions as a spatially distributed patchy population at Fort McCoy, and not as a classic metapopulation contradicting the suggestion of Givnish et al. (1988). An important characteristic of a classic metapopulation is that its component populations fluctuate asynchronously (Levins 1970). The eleven subpopulations at Fort McCoy did not fluctuate asynchronously from 1997 to 2003. In the main lupine area of the south Fort, populations were synchronous in the short-term and showed a synchronized long-term trend, declining from the summer flight in 1997 to spring flight in 1999 and then gradually increasing from the summer flight in 1999 to the spring in 2003. It is possible that this trend is part of a long-term population cycle with a half period length of approximately two and half years, or it maybe a feature unique to this time period. It is unlikely this trend is due to specific management activities because management has been site specific and does not readily correlate with the observed long-term dynamics (Appendix A: Fig. 1; Wilder 1999). Populations in the north Fort probably had different dynamics from the south Fort. Only two of the five north sites trended similar to those in the main south Fort. Two other north sites had constant populations and one seemed to be increasing. However, none of these patterns in the north Fort were asynchronous.

If, historically, Karner blue butterflies existed as a classic metapopulation, in modern times it has been converted to a patchy population structure via human interventions and management of the landscape (see Appendix A for additional discussion). In Wisconsin, humans may have deliberately or inadvertently changed the landscape to reduce the natural extirpation rate (while substituting anthropogenic factors), and increasing persistence of subpopulations. Such human induced shifts in population structure maybe quite common both for the Karner blue butterfly and other species. Recognizing this shift may assist researchers better understand applied aspects of metapopulation theory.

Our findings also suggest that Karner blue butterfly populations at Fort McCoy appear to be non-declining or stable. Several more years of data are needed to confirm this suggestion, but it is likely that the north and south areas of the Fort can be managed as independent units as suggested in this species' Recovery Plan (U.S. Fish and Wildlife Service 2003). It is also possible that populations in the southwest corner of the Fort and associated populations on the nearby privately held lands also function independently of the main south Fort area, but additional evidence is needed. Our analysis suggests that populations at Fort McCoy may soon meet the criteria (U.S. Fish and Wildlife Service 2003) to be desig-

nated as large viable metapopulations, and that Fort McCoy maybe a good location for further studies to characterize suitable habitat of Karner blue butterfly.

Annual population change

Dramatic population fluctuations from year to year are a common characteristic for insect species (Miyashita 1963; Ito 1980) and these create conservation challenges (Schultz & Chang 1998). Previous research on Karner blue butterfly has suggested that the summer flight is typically three to four times higher than the preceding spring flight, although in some years the summer flight is smaller than the spring flight (U.S. Fish and Wildlife Service 2003). Due to the high variability among years, as observed at Fort McCoy, the mean net population growth rate can be misleading; instead we suggest that it is essential to understand the factors that generate the high variability amongst years rather than rely on a single number describing the average change between the generations.

Negative density-dependent population growth was commonly observed during the summer and only rarely detected over the winter (Fig. 2). The strength of density-dependence varied considerably among years, and we were unable to find any weather factor that explained this variation (for additional discussion on population growth and weather variables see Appendix A). Several researchers have found that Karner blue larvae thrive on higher quality *L. perennis* found in partially or fully shaded subhabitats (Grundel, Pavlovic, & Sulzman 1998; Maxwell 1998; Lane & Andow 2003). In years with high butterfly density there maybe an inadequate density of oviposition sites in partially and fully shaded subhabitats. Therefore a higher proportion of spring adults may lay eggs on lower quality *L. perennis* and this may result in lower larval survival rates. Other factors may also be important including variation in nectar (Boggs 1987) and tending ants that increase larvae survival (Savignano 1994).

The density-independent, significant positive correlation between higher rainfall in June and July and higher summer net population growth rate might have been mediated through microclimate and water stress of the host plant, *L. perennis*. Grundel et al. (1998) and Lane (1999) found that Karner blue larval development time was slower on wilted *L. perennis* leaves than on leaves from well-watered plants, higher precipitation would likely result in lower lupine water stress resulting in higher larvae survival.

Broader implications

The type of metapopulation structure affects how recovery activities for an endangered species are prioritized, which in turn may affect prospects for long-term recovery. If an endangered species has a classic metapopulation structure, then management for recovery would require monitoring population size of all subpopulations and attention to maintaining

and monitoring appropriate dispersal corridors between patches. In comparison, a core-satellite structure would focus management efforts to ensure that the core persists, while a patchy population would enable even less-focused efforts. Monitoring a patchy metapopulation would likely involve sampling fewer patches and would be less time consuming than monitoring a classic metapopulation. We suggest that aiming to recover core-satellite or patchy metapopulations will reduce monitoring costs, simplify reserve design, and create more robust populations, which are more likely to persist into the future.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2009.09.006.

References

Andow, D. A., Baker, R. J., & Lane, C. P. (Eds.). (1994). *Karner blue butterfly: A symbol of a vanishing landscape*. St. Paul: Minnesota Agricultural Experiment Station.

Baguette, M. (2004). The classical metapopulation theory and the real, natural world: A critical appraisal. *Basic and Applied Ecology*, *5*, 213–224.

Boggs, C. L. (1987). Ecology of nectar and pollen feeding in Lepidoptera. In F. J. Slansky, & J. G. Rodriguez (Eds.), *Nutritional ecology of insects, mites, spiders, and related invertebrates* (pp. 369–391). New York: John Wiley and Sons.

Boorman, S. A., & Levitt, P. R. (1973). Group selection on the boundary of a stable population. *Theoretical Population Biology*, *4*, 85–128.

Brown, J.A., & Boyce, M.S. (1996). Monitoring of Karner blue butterflies (*Lycaeides melissa samuelis*) for the proposed Habitat Conservation Plan, Wisconsin. Report to the US National Fish and Wildlife Foundation.

Ehrlich, P. R., White, R. R., Singer, M. C., McKechnie, S. W., & Gilbert, L. E. (1975). Checkerspot butterflies: A historical perspective. *Science*, *188*, 211–228.

Givnish, T. J., Menges, E. S., & Schweitzer, D. F. (1988). *Minimum area requirements for long-term conservation of the Albany Pine Bush and Karner blue butterfly: An assessment*. Albany, NY: Report to the City of Albany from Malcolm Pirnie, Inc.

Grundel, R., Pavlovic, N. B., & Sulzman, C. L. (1998). The effect of canopy cover and seasonal change on host plant quality for the endangered Karner blue butterfly (*Lycaeides melissa samuelis*). *Oecologia*, *114*, 243–250.

Guiney, M. S., & Andow, D. A. (2009). Long lifetime of a male Karner blue butterfly, *Lycaeides melissa samuelis* (Lycaenidae) in Minnesota. *Entomological News*, *120*, 107–108.

Hanski, I. (1991). Single-species metapopulation dynamics: Concepts, models and observations. *Biological Journal of the Linnean Society*, *42*, 17–38.

Hanski, I. (2004). Metapopulation theory, its use and misuse. *Basic and Applied Ecology*, *5*, 225–229.

Hanski, I., Moilanen, A., Pakkala, T., & Kuusaari, M. (1996). The quantitative incidence function and persistence of an endangered butterfly metapopulation. *Conservation Biology*, *10*, 578–590.

Harrison, S., Murphy, D. D., & Ehrlich, P. R. (1988). Distribution of the bay checkerspot, *Euphydryas editha bayensis*: Evidence for a metapopulation model. *The American Naturalist*, *132*, 360–382.

Hastings, A., & Harrison, S. (1994). Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics*, *25*, 167–188.

Husband, B. C., & Barrett, S. C. H. (1996). A metapopulation perspective in plant populations. *The Journal of Ecology*, *84*(3), 461–469.

Ito, Y. (1980). *Comparative ecology*. Cambridge, United Kingdom: Cambridge University Press.

Lafferty, K. D., Swift, C. C., & Ambrose, R. F. (1999). Extirpation and recolonization in a metapopulation of an endangered fish, the tidewater goby. *Conservation Biology*, *13*, 1447–1453.

Lane, C.P. (1999). *Benefits of heterogeneous habitat: Oviposition preference and immature performance of Lycaeides melissa samuelis Nabokov (Lepidoptera: Lycaenidae)*. Ph.D. dissertation. University of Minnesota, St. Paul.

Lane, C. P., & Andow, D. A. (2003). Oak savanna subhabitat variation and the population biology of *Lycaeides melissa samuelis* (Lepidoptera: Lycaenidae). *Annals of the Entomological Society of America*, *96*(6), 799–809.

Lawes, M. J., Mealin, P. E., & Piper, S. E. (2000). Patch occupancy and potential metapopulation dynamics of three mammals in fragmented afromontane forest in South Africa. *Conservation Biology*, *14*, 1088–1098.

Levins, R. (1970). Extinction. *Lectures on Mathematics in the Life Sciences*, *2*, 75–107.

Marsh, D. M., & Trenham, P. C. (2001). Metapopulation dynamics and amphibian conservation. *Conservation Biology*, *15*(1), 40–49.

Manly, B. F. J. (1976). Extensions to Kiritani and Nakasuji's method for analysing insect stage-frequency data. *Population Ecology*, *17*(2), 191–199.

Maxwell, J.A. (1998). *The conservation of the Karner blue butterfly (Lycaeides melissa samuelis Nabokov)*. Ph.D. dissertation. University of Wisconsin, Madison.

Miyashita, K. (1963). Outbreaks and population fluctuations of insects, with special reference to agricultural insect pests in Japan. *Bulletin of the National Institute of Agricultural Sciences, Series C*, *15*, 99–170.

Opdam, P. (1991). Metapopulation theory and habitat fragmentation: A review of holarctic breeding bird studies. *Landscape Ecology*, *5*, 93–106.

Royama, T. (1992). *Analytical population dynamics*. New York: Chapman and Hall.

SAS Institute, I. (1997). *SAS user's guide: Statistics*. Cary, NC: SAS Institute, Inc.

Savignano, D. A. (1994). Benefits to Karner blue butterfly from association with ants. In D. A. Andow, R. J. Baker, & C. P. Lane (Eds.), *Karner blue butterfly: a symbol of a vanishing landscape* (pp. 37–46). St. Paul: Minnesota Agricultural Experiment Station.

Schultz, C. B., & Chang, G. C. (1998). Challenges in insect conservation: Managing fluctuating populations in disturbed environments. In P. Fiedler, & P. Kareiva (Eds.), *Conservation biology for the coming decade* (pp. 228–254). New York: Chapman and Hall.

Schweitzer, D. F. (1994). Prioritizing Karner blue butterfly habitats for protection activities. In D. A. Andow, R. J. Baker, & C. P. Lane (Eds.), *Karner blue butterfly: A symbol of a vanishing landscape* (pp. 173–184). St. Paul: Minnesota Agricultural Experiment Station.

Turchin, P., & Taylor, A. D. (1992). Complex dynamics in ecological time series. *Ecology*, *73*(1), 289–305.

U.S. Fish and Wildlife Service. (2003). *Karner blue butterfly (Lycaeides melissa samuelis) recovery plan*. Minnesota: Fort Snelling., p. 221

Watermolen, D. J., Bleser, C., Zastrow, D., Christenson, J., Lentz, D. R., Wood, D., et al. (2000). *Wisconsin statewide Karner blue butterfly habitat conservation plan and environmental impact statement*. Madison: Wisconsin Dept. Natural Resources., 386 pp. + 8 appendices. Available at http://dnr.wi.gov/forestry/karner/hcptext/ Accessed 5.06.08

Wilder, T. T. (1999). *Fort McCoy Karner blue butterfly endangered species management plan*. Fort McCoy: United States Department of Defense.